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Formica nigricans Emery, 1909 — an ecomorph of *Formica pratensis* Retzius, 1783 (Hymenoptera, Formicidae)

Bernhard Seifert

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Workers and queens from 224 nest samples of *Formica pratensis* Retzius originating from all over Europe, but mainly from Germany were investigated for several morphological characters, particularly pilosity. Statistic differences between the hairy N morph (= *F. nigricans* Emery 1909) and the less hairy P morph in body size, pilosity, geographic frequency, habitat selection and mound construction could be shown but other aspects of external biology coincide. There are no suggestions of reproductive isolation of the morphs which are interpreted as different genotypes of the same population and represent different ecological adaptions. The strong decrease of N morph frequency in *pratensis* populations from S to N Europe, its higher frequency in more xerothermous habitats in Germany, and its well-documented peculiarity of constructing higher mounds than the P morph for conditions of equal sun-exposure characterize the N morph as a genotype adapted to higher temperatures. In Germany, as much as 16 % of *pratensis* nests investigated contained both morphs. Polycalic colonies are found in both morphs but isolated nests predominate. *Formica minor pratensoides* Gößwald 1951 is a synonym of *pratensis* and refers to polycalic colonies of the P morph which occasionally occur inside more mesophilic, less sun-exposed forests.

Bernhard Seifert, Staatliches Museum für Naturkunde Görlitz, D0-8900 Görlitz, Am Museum 1, Germany

1. Introduction

There has been an everlasting controversy on the species status of *Formica rufa pratensis* var. *nigricans* described by Carlo Emery in 1909. Among the later myrmecologists who argued for a separate species status of *nigricans* were Kutter (1977) and Collingwood (1979), while Dlusskii (1967) and Paraschivescu (1972) refused to accept this interpretation. When beginning my studies on this matter, I was biased towards the view that *pratensis* and *nigricans* were sympatric, reproductively isolated biospecies. Habitat selection, geographic distribution and pilosity data seemed to favour this point of view. However, after 12 years of sampling, field observations and morphological studies, I was forced to give up this hypothesis and to regard *nigricans* now as a hairy morph (or genotype) of Formica *pratensis* with differing etho-ecological adaptions.

2. Material and methods

The ant material investigated originated from S Sweden, S Finland, Denmark, the Netherlands, Germany, Poland, Czechoslovakia, France, Switzerland, Hungary, Romania, the Ukraine, Bulgaria, Greece, Italy and Spain — provided by Per Douwes, Heikki Wuorenrinne, Cedric Collingwood, Volker Assing, Volker Hauck, Petr Werner, Pavel Bezdecka and Gennady Dlusskii, whose friendly support I want to acknowledge here with grateful thanks. The majority of samples, however, were taken by the author, mainly in the German provinces of Sachsen, Thüringen, Sachsen-Anhalt, Brandenburg and Mecklenburg-Vorpommern. The material investigated morphologically included 224 nest samples with 1756 workers and 295 queens. In the case of higher intranidal variability, more than the standard 7 workers per nest were investigated.

The following morphological characters were studied in workers:

HW: maximum measurable head width (normally slightly behind eyes but in smaller workers across eyes)

NBH: number of standing hairs on one half of occipital margin frontad to eye level and seen in straight dorsal view. In case of bilateral asymmetries, both halves are counted and the number divided by 2

LBH: length of longest hair on occipital margin of head seen in straight dorsal view. Hairs on ventral occiput are not considered

NHTI: number of standing hairs on extensor profile of hind tibia

As "standing hairs" were understood only those hairs which project more than 11 µm from cuticular surface. Initially, two additional characters, pronotal and gaster hair lengths, were investigated but these did not notably help to separate the two morphs and were neglected. The same was true of the scape and head ratios, which did not differ significantly in a test on 40 nest samples — a result that is confirmed by Dlusskii (1967). For easier and uniform presentation, all measurements are given in µm, even for HW where an accuracy of ± 1 µm is impossible.

The following morphological characters were studied in queens:

HW: maximum measurable head width

NBH: as in worker, but only hairs projecting > 55 µm from cuticular surface were considered

LBH: as in worker, but a slight tilt to measure full hair length is allowed

NSCU: number of standing hairs projecting > 55 µm from cuticular surface of scutellum

LSCU: length of longest standing hair on scutellum

NPP: number of standing hairs projecting > 55 µm from propodeal profile line when seen in lateral view

LPP: length of longest standing hair on propodeum

NHTI: number of standing hairs on distal half of extensor profile of hind tibia if projecting > 11 µm

LHTI: length of longest hair on whole extensor profile of hind tibia, a slight tilt to measure full hair length is allowed

NGA: counted in lateral view: number of standing hairs projecting > 55 µm from cuticular surface of the frontal face of first gaster tergite dorsad to the level of upper margin of petiole scale

LGA: length of longest hair on frontal face of first gaster tergite.

3. Morphology

3.1. Workers

The pilosity data NBH (Fig. 1), LBH and NHTI showed highly positive correlations for the pooled material of both morphs with 1756 correlated workers: NBH/LBH 0.594, NBH/NHTI 0.572 and LBH/NHTI 0.484. This justifies a multiplicative computation of data as applied in the calculation of the discriminant D(3) as presented below. The correlations within the 2 morphs (*nigricans* morph = N morph, *pratensis* morph = P morph) were lower for each data pair than the pooled correlations. This is a first, weak, suggestion for conspecifity since we might normally expect higher correlations within a species than in a sample made up of different species. The correlation coefficients were NBH/LBH 0.421, NBH/NHTI 0.229 and LBH/NHTI 0.223 for 962 workers of the P morph and NBH/LBH 0.391, NBH/NHTI 0.422 and LBH/NHTI 0.346 for 794 workers of the N morph. To remove the body-

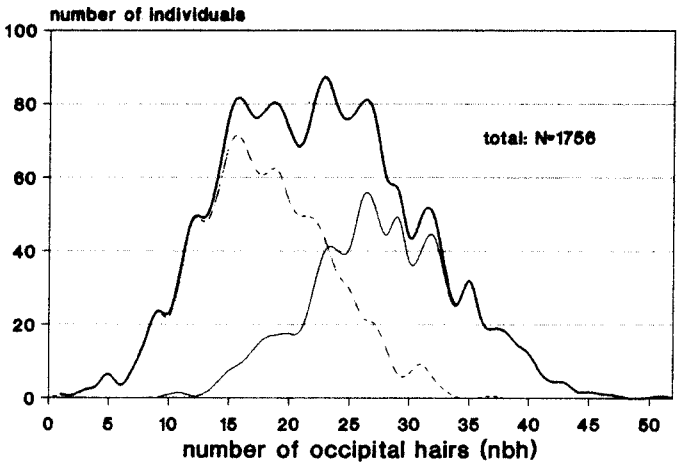

Fig. 1. Distribution of the unilateral number of occipital hairs (NBH) in worker individuals of *Formica pratensis*. — Dashed line = P morph; thin, solid line = N morph; thick, solid line = both morphs.

size-dependent variability of pilosity data, diphasic correction functions were calculated. These corrections were at first calculated for each morph separately and then averaged to one function. This two-step procedure was necessary because the body size distributions of both morphs differed. The correction functions NBH(HW), LBH(HW) and NHTI(HW) share for both morphs the common character to reduce the slope for larger head widths. The averaged correction functions are

NBH(HW) = 0.009379 HW + 6.402
for HW ≥ 1726,
NBH(HW) = 0.006662 HW + 11.092
for HW ≥ 1726,
LBH(HW) = 0.06112 HW + 19.06
for HW < 1778,
LBH(HW) = 0.02343 HW + 86.8
for HW ≥ 1778,

NHTI(HW) = 0.007837 HW + 7.614
for HW < 1787, and
NHTI(HW) = 0.004571 HW + 13.452
for HW ≥ 1787.

The corrected pilosity data NBH_{cor} LBH_{cor} and $NHTI_{cor}$ were calculated as

NBH_{cor} = NBH / NBH(HW),
LBH_{cor} = LBH / LBH(HW), and
$NHTI_{cor}$ = NHTI / NHTI(HW).

Table 1 gives a comparison of the crude and corrected data of both morphs. Defining a coefficient of separation as

$$|mean_1 - mean_2| / (SD_1 + SD_2)$$

and comparing the geometric mean of the crude data with the geometric mean of the size-corrected data [the index D(3)], the separation of

Table 1: Morphometric data (mean ± *SD*, range) of individual workers of 2 morphs of *Formica pratensis*. Given are head width, crude and size-corrected pilosity data, and the discriminant D(3) as geometric mean of the 3 corrected data. All means are significantly different for $P < 0.0001$.

	N morph (n = 794)		P morph (n = 962)	
HW	1771.8 ± 218.5	1046 – 2185	1815.9 ± 217.5	1047 – 2249
NBH	28.17 ± 6.42	10 – 51	17.87 ± 5.74	1 – 37
LBH	140.6 ± 20.1	55 – 231	109.7 ± 26.2	50 – 209
NHTI	25.12 ± 5.11	9 – 45	17.83 ± 5.21	2 – 42
NBH_{cor}	1.24 ± 0.27	0.55 – 2.49	0.77 ± 0.24	0.04 – 1.60
LBH_{cor}	1.13 ± 0.18	0.42 – 1.87	0.87 ± 0.19	0.37 – 1.65
NHT_{cor}	1.18 ± 0.22	0.43 – 2.04	0.83 ± 0.23	0.10 – 1.82
D(3)	1.17 ± 0.17	0.60 – 1.75	0.81 ± 0.16	0.20 – 1.30

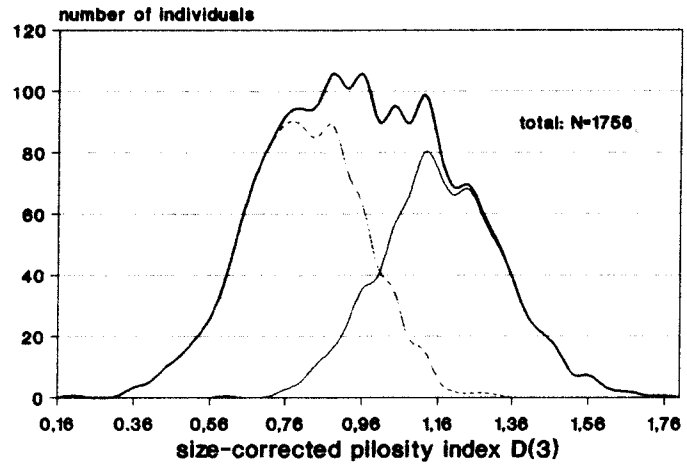

Fig. 2. Distribution of the size-corrected pilosity index D(3) for individual workers of *Formica pratensis* calculated as geometric mean of the size-corrected pilosity data NBH_{cor}, LBH_{cor} and $NHTI_{cor}$. — Dashed line = P morph; thin, solid line = N morph; thick, solid line = both morphs.

both morphs is improved from 0.98 to 1.124 (Fig. 2) or, in other terms, the size-correction reduces the area overlap of frequency distributions from 32 to 26 %. The HW means in Table 1 are most probably larger than the real values because the methods of sampling and morphological investigation induced a certain tendency to neglect the smallest workers. However, the largest head width HW_{max} within a sample was recorded realistically. For 106 nest samples of the N morph HW_{max} is 1971.1 ± 149.3 and for 118 nests of the P morph 2021.0 ± 127.4. This difference is significant for $P < 0.01$ and confirms the situation indicated by the means in Table 1. It should be noted that the fraction of largest workers with HW > 2150 is almost absent in the N morph (0.38 % of individuals but more frequent in the P morph (3.01 %).

An explanation of how the identification of morphs was made is necessary here:

The starting point for a separation of entities was a subjective either/or assessment of which nests most probably belong to the hairy N morph or to the less hairy P morph. Then preliminary frequency distributions were separately computed for each subjective morph. In a second step, all nest samples were related to these preliminary frequency distributions and their morph allocation reassessed. This reassessment was performed according to the position of a nest sample in the preliminary frequency distribution of D(3). Samples having D(3) smaller than the threshold of equal probabilities, which is marked by the intersection point of the distributions, were reallocated to the P morph and samples with larger D(3) to the N morph. With the data of the reallocated samples further frequency distributions were calculated and further reallocations were performed until a stable state was achieved. In the case of nest samples, the point of equal probabilities was at D(3) = 0.97 (Fig. 3). This iterative, self-organizing process the starting point for which is set by a subjective decision should be a powerful discriminant method in taxonomy. The method is expected to compute the same final state even if the initial hypothesis is less close to reality.

3.2. Queens

The pilosity data of 295 queens show highly positive correlations (Table 2) which justifies a multiplicative computation of discriminants. As in workers, the correlations are notably smaller within the morphs than in the pooled sample. The frequency distributions of each pilosity character are as regards their basic shape very similar: there is a very pronounced, steep peak at very low or zero values representing the P morph and a very extended, flat curve at higher values representing the N morph. A demarkation line between the morphs is often poorly defined. Fig. 4 and Fig. 5 give an average, and a more clear, example. The distribution of the pilosity index D(10) computed as the square root of a ten-

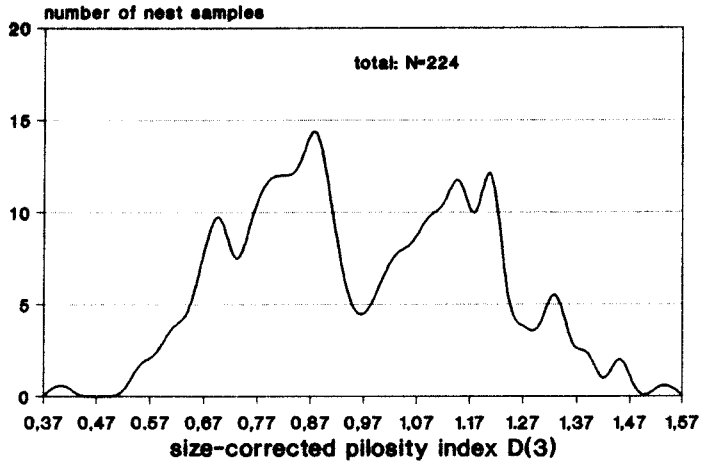

Fig. 3. Distribution of nest sample means of the size-corrected pilosity index D(3) for workers of *Formica pratensis*. The left peak with D(3) < 0.97 is regarded as the P morph and the right peak with D > 0.97 as the N morph.

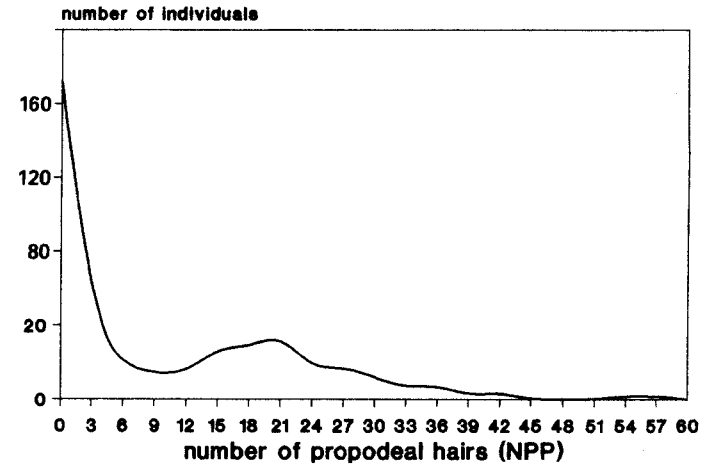

Fig. 4. Distribution of the numbers of standing hairs seen on propodeal profile (NPP) in queens of *Formica pratensis*. The left, steep peak represents the P morph and the right flat distribution the N morph. Similar types of distribution are found in the 4 other pilosity characters NBH, NSCU, NGA and NHTI.

Table 2: Linear correlation coefficients of 10 pilosity characters in 295 queens of *Formica pratensis*.

	NBH	LSCU	NSCU	LHTI	NHTI	LPP	NPP	LGA	NGA
LBH	0.814	0.750	0.835	0.891	0.859	0.802	0.846	0.656	0.814
NBH	—	0.572	0.835	0.781	0.814	0.652	0.837	0.511	0.689
LSCU		—	0.728	0 779	0.702	0.853	0.676	0.848	0.870
NSCU			—	0.835	0.845	0.766	0.875	0.648	0.820
LHTI				—	0.891	0.789	0.842	0.677	0.828
NHTI					—	0.746	0.852	0.629	0.799
LPP						—	0.755	0.806	0.877
NPP							—	0.611	0.798
LGA								—	0.836

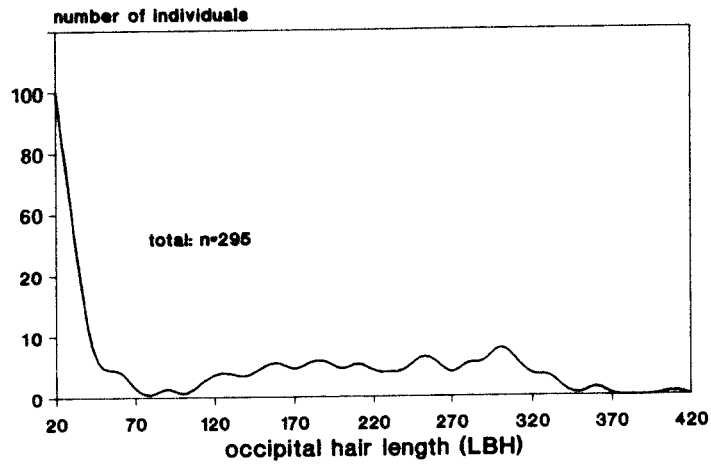

Fig. 5. Distribution of occipital hair length (LBH) in queens of *Formica pratensis*. The left, steep peak represents the P morph and the right, flat distribution the N morph. Similar types of distribution are found for the 4 other hair length characters LSCU, LPP, LHTI and LGA.

character geometric mean suggests that queens with D(10) < 4.3 might be considered as P morph individuals and queens with D(10) ≥ 4.3 as N morph individuals. The sorting presented in Table 3 was performed according to this 4.3 threshold. This is to some degree an arbitrary decision since the range of uncertainty extends from about 4.0 to 5.8 (Fig. 6) but from the composition of nest samples and simultaneous consideration of the associated worker phenotypes it seems a reasonable fixation. To avoid zero values of D(10), pilosity numbers of 0 were transformed to 0.1 and pilosity lengths of 0 transformed to 27 µm.

Similar to the situation in workers, the hairy N morph has a significantly smaller head width. 9 % of P morph queens are larger than the largest N morph queen.

Of particular interest is the intranidal morph composition. As stated above, queens with D(10) < 4.0 and D(10) > 5.8 represent with high probability different morphs. Among 37 nest samples as much as 8 (= 21.6 %) contained simultaneously morphs with D(10) < 4.0 and D(10) > 5.8. The substantial number of 6 nests (= 16.2 %) contained simultaneously queens with D(10) < 2.7 and D(10) > 7.0! These remarkably high proportions of mixed nests are a clear indication that both morphs are provided by the same gene pool and do not represent reproductively isolated species. Dlusskii (1967) and Paraschievescu (1972) have

Table 3: Morphometric data (mean ± *SD*, range) of 2 morphs of *Formica pratensis* queens. The means of HW differ significantly for $P < 0.0001$. The pilosity data differ for $P << 0.01$ according to a nonparametric Mann-Whitney *U* test.

	N morph (n = 123)		P morph (n = 172)	
HW	2253.1 ± 68.7	2036 – 2401	2293.4 ± 83.1	2094 – 2512
LBH	217.6 ± 82.5	27 – 403	30.0 ± 20.0	0 – 247
NBH	16.17 ± 14.13	0 – 50	0.17 ± 0.76	0 – 10
LSCU	356.2 ± 38.2	135 – 453	91.4 ± 110.7	0 – 388
NSCU	24.7 ± 13.6	1 – 80	1.13 ± 2.45	0 – 17
LHTI	192.0 ± 67.2	43 – 341	36.2 ± 20.5	0 – 134
NHTI	8.38 ± 4.30	1 – 16	0.64 ± 1.03	0 – 6
LPP	258.2 ± 58.6	98 – 377	64.8 ± 73.4	0 – 308
NPP	17.72 ± 11.08	0 – 57	0.23 ± 0.56	0 – 5
LGA	333.3 ± 34.5	226 – 423	147.8 ± 112.7	0 – 368
NGA	47.62 ± 12.4	20 – 75	8.49 ± 11.67	0 – 48

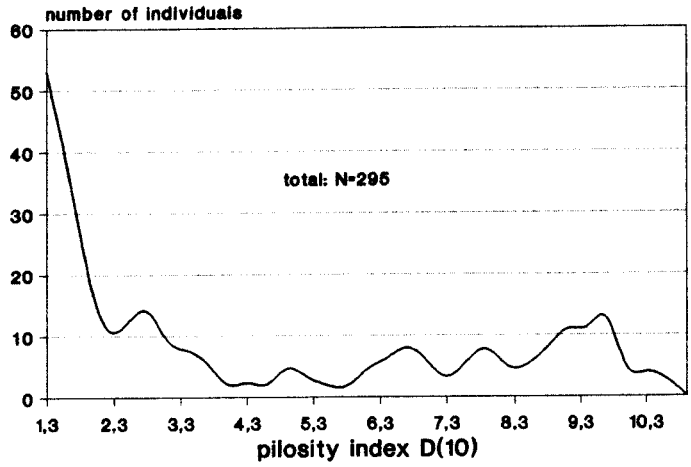

Fig. 6. Distribution of the square root transformed geometric mean D(10) of the 10 pilosity characters LBH, NBH, LSCU, NSCU, LHTI, NHTI, LPP, NPP, LGA and NGA in queens of *Formica pratensis*. Specimens with D(10) < 4.0 represent the P morph and such with D(10) > 5.8 the N morph.

already referred to the occurrence of mixed nests but since there was no extensive study of queen nest samples it has remained unknown how abundant these really were and it is difficult to give a convincing demonstration of a mixed nest using workers because the morphs' pilosity differences are much less in this caste.

4. Ecology and distribution

The abundance ratio of the N morph against the P morph in Europe shows the general geographic trend to grow from north to south. In S Bulgaria, Greece and Italy the N morph clearly predominates (about 5:1) but this ratio is inverted in the northern parts of the *F. pratensis* range. The N morph is reported to be completely absent from the British Isles (Collingwood 1979) and probably goes no farther north than 58°N in Scandinavia and 60°N in Finland (according to Collingwood and my own results). The P morph is reported from Scandinavia and Finland up to 63°N. In Germany the N/P ratio is about 1:2; my own studies confirmed the N morph for 37 localities and the P morph for 77 localities. This change in morph frequency from north to south is confirmed by Dlusskii (1967) who reports an absolute predominance of the N morph in the hot mountain steppes of Soviet Central Asia. The habitat selection of both morphs in Germany shows some obvious differences. The most notable difference is perhaps in the soil class of the nest sites (Table 4). The P morph has a tendency to occur in less dry and less warm situations compared to the N morph. About 19 % of P nests were found on loamy soils but only 3 % of the recorded N nests (difference significant for $P < 0.01$ in a χ^2-test). As a consequence, the N morph is nearly absent and replaced by the P morph in regions were brown soil types predominate: the mountains and forelands of the Lausitzer Gebirge, Erzgebirge and Harz. 10 % of P morph nests occurred on loess soils where no N nests were found ($P < 0.01$, χ^2). Both morphs are found on limestone soils (mainly rendzinas, sometimes protorendzinas) but the N morph is here significantly ($P < 0.01$, χ^2) more abundant than the P morph, i.e. 54 % against 29 %. The frequency of the morphs is equal on sandy soils (both 42 %), but here a tendency to

Table 4. Soil classes (%) at nest spots of the N and P morph of *Formica pratensis*. Except for the soil class "sand", which is equally frequent in both morphs, all remaining soil classes differ between the morphs for $P < 0.01$.

Soil class	Nest spots:	P morph 90	N morph 87
Sand		42	43
Limestone		29	54
Loam		22	3
Loess		10	–

prefer different plant communities seems to exist. The P morph was more frequently found in sandy heathlands dominated by *Pinus*, *Betula*, *Vaccinium* and *Calluna* but the N morph dominated in sandy xerothermous grasslands with high plant diversity in the field layer. Hence the N morph is characteristic for the sandy hills of many nature conservancy areas in Mecklenburg-Vorpommern and Brandenburg (e.g. Geesower Hügel, Silberberge near Gartz, Feißnecksee near Waren).

The geographic distribution in Europe and the observed differences in habitat selection infer an adaptation of the N morph to higher temperatures. This conclusion is supported by a remarkable behavioural adaptation which has been demonstrated by Dlusskii (1967) for the first time. Dlusskii studied a *Formica pratensis* population in the Woronesh Nature Conservancy Area and found the N morph to construct significantly steeper nest mounds than the P morph for equal incidence of direct sunlight on nest spots.

My own investigations confirmed Dlusskii's observations fully: to give comparable solar inclinations, the observations were confined to areas between latitudes 48° and 52°N. Samples of doubtful morph identity were excluded and a total of 26 N morph and 28 P morph nests investigated for height (H) and radius (R) of the virtual organic mound (i.e. excluding collars or ejections of mineral soil). The horizon was mapped for shadow-producing structures in the directions E, SE, S, SW and W. With these data and using astronomic maps, the potential amount of direct sunlight reaching the nest spot during a defined spring day was calculated. If S means the amount of daily sunlight (S = 1.0 means full exposure, S = 0 total shadow) and tan a means the ratio H/R of the sun-exposed mound slope, the following regression functions are computed:

P morph: $\tan a = -0.6521\, D + 0.6750$
($n = 28$, $r = -0.5584$, $P < 0.01$)
N morph: $\tan a = -0.9366\, D + 1.1794$
($n = 26$, $r = -0.6206$, $P < 0.001$).

For 20 % daily sunlight, the regressions predict a mound slope of 45° for the N morph and of 29° for the P morph. For conditions of full exposure, the predicted mound slopes are 14° for the N morph and only 1° for P morph.

Even the most hairy workers of the N morph have by no means the pilosity of a bumblebee. However, it seems not unlikely that the longer and more numerous pilosity of the N morph provides at least a small protection against air movements above the cuticular surface. On the other hand the erect pilosity is dilute enough to allow a sufficient cuticular absorption of solar energy or even to facilitate this process by centripetal reflection or the cable-like transport of sunlight. The extension of black pigmentation, which has given the N morph its scientific name of "*nigricans*" is highly variable and shows no consistent difference from the P morph, but the black spot on the mesosoma is on average more extended in the German N morph worker. This may be regarded as a further morphological adaptation to improve energy absorption. For desert ants, Dlusskii (1981) has demonstrated the significance of cuticular structures and pigmentation for reflection, absorption and transmission of solar energy.

The deviations in distribution, habitat selection and mound construction stated above were the only detectable non-morphological differences. In other external aspects of biology both morphs are very similar, if not equal. Both have monocalic and polycalic colonies, both incise stable runways into the turf of grasslands by cutting off grasses and smoothing the ground. Among all European wood ants, both have the strongest tendency to exploit food resources in dense grasslands and to forage in the field layer (probably the N morph is slightly better adapted for foraging in high and thin field layer plants because, in contrast to the P morph, the fraction of largest workers with HW > 2150 is almost absent). Finally, both morphs differ from all European wood ant species in having 2 separate flight periods in May/June and in August.

A comment is necessary on polycalic colonies inside woodlands which were observed in 4 P morph and in 2 N morph localities. The invasion of woodland sites with substantially lower sun-exposure on the ground and the lack of *Formica fusca* group nests causes problems for a thermophilic species which normally inhabits forest margins or open land and which frequently founds colonies in a socialparasitic way in members of the *Formica fusca* group. A normal and intelligi-

ble response of *Formica pratensis* to the changed environment is to enlarge the number of queens and the worker population of the nest and to found new nests by budding from a mother colony. Larger nest populations are able to produce higher core temperatures in the mounds by metabolic heat production which compensates for the losses of direct solar energy and the budding makes them independent from *fusca* group nests. The nest mounds, being flat in open situations, are here built larger and steeper for the better collection of sunlight and now resemble the *rufa* group mounds. Indeed, such polycalic and very populous colonies in woodland sites, which have smaller workers as a result of higher queen ratios and which have different nest materials as a result of smaller worker size and a differing botanic environment, convey the overall impression of being another species.

The moment I found, as an unexperienced beginner of myrmecology, my first polycalic colony of *Formica pratensis* in a spruce forest in the Harz mountains I was excited, believing I had made the first record of *Formica lugubris* for NE Germany. The subsequent microscopic investigation of workers and queens destroyed this splendid thought completely. This anecdote elucidates the possible failures of a "wood ant guru" who is not able to see and investigate microscopic structures. So the often-cited *Formica minor pratensoides* Gößwald 1951 is nothing but the P morph of *Formica pratensis* which has shifted in spruce forests to polycalic colony structures. Ant material from Dormagen/Nordrhein-Westfalen determined by Gößwald himself as *Formica pratensoides* is structurally identical with the P morph. Responding to an inquiry for type specimens of *pratensoides*, Gößwald wrote "... Durch Kriegsereignis ist mein gesamtes Sammlungsmaterial verlorengegangen ..." (letter of 29 January 1985). This must be a mistake since the original *pratensoides* material was collected in 1947–49 (Gößwald 1951).

In all inner forest sites with polycalic colonies of *F. pratensis* no nests of the *F. rufa/polyctena* complex were observed nearby. This clearly indicates that the success of *Formica pratensis* inside forests is largely dependent on the absence of superior wood ant competitors. The fact that one of Gößwalds "*pratensoides*" colonies disappeared soon after he had artificially introduced *Formica rufa polyctena* to this site (Gößwald 1951) provides further evidence for the competitive inferiority of *pratensis* inside forests. No significant difference of the *pratensis* morphs in frequency of polycalic colonies was demonstrable; in Germany, polycalic colonies were found in 5 out of 61 P morph sites (= 8 %) and 5 out of 31 N morph sites (= 16 %).

5. Evidence for conspecifity of both morphs

Above, morphological evidence for conspecifity of both morphs was presented with the high ratio of mixed nests. Ecological and ethological arguments can be added.

Investigating the chorology and ecological potency of the highly similar species *Lasius flavus / myops*, *Lasius jensi / meridionalis*, *Lasius niger / platythorax*, *Formica cunicularia / rufibarbis*, *Tetramorium caespitum / impurum*, *Myrmica rubra / ruginodis*, *Tapinoma erraticum / ambiguum* and of 3 German sibling species of Lasius "alienus" (Seifert 1983, 1984, 1984, 1987, 1988, 1991a and in prep.), the general validity of a basic ecological rule among Central European ants could be shown. This rule means that species of highest morphological similarity have a large overlap of their fundamental niche spaces (or high similarity of their basic ecological potencies) but tend to minimize the overlap of their realised niche spaces (i.e. to minimize the frequency of syntopic occurrence). Figures typical for these 8 species pairs are 60–70 % overlap of fundamental niches but only 2–15 % overlap of realised niches. The P and N morph have undoubtedly a high similarity in basic ecological requirements and, if they were different species, mechanisms or factors for spatial segregation should function to avoid the high costs of competition or crossbreedings (Seifert 1986, 1987). Precisely this segregation of the P and N morphs is not given. For 20 sites with at least 3 recorded *pratensis* nests per site and a total of 105, a realised niche overlap of 39.4 % was calculated. This is by no means the situation typical for a pair of sibling species. Sometimes, single nests of the one morph were found amidst a nest clus-

Through war events is my collected type material lost."

ter of the other morph. These chorological findings are confirmed by Dlusskii (1967) who wrote "... over almost the whole territory of the USSR where *pratensis* is found but on each spot where sufficiently large sampling was performed, both forms were encountered — except for Soviet Central Asia, where only the hairy form is found ..." (free translation from Russian).

I have two direct observations of nuptial flights which add to the argument against reproductive isolation of the morphs: N and P morph queens flying simultaneously above the same spot of a xerothermous grassland slope (Thüringen/Germany, May 1984), and N and P morph queens and P morph males gathering for mating on the same moss pad of a meadow slope (Sierra de Gredos/Spain, May 1991). In the latter case the sexuals must have made at least a medium-range flight since the closest nest was 80 m away.

To sum up the present knowledge the following synonymic synopsis may be given:

Formica pratensis Retzius, 1783

Formica pratensis var. *nigricans* Bondroit, 1912. [First available use of the unavailable infrasubspecific name *F. rufa* subsp. *pratensis* var. *nigricans* Emery, 1909].

F. nigricans; Yarrow, 1955 (as valid species). [*F. nigricans* most recently treated as a junior synonym of pratensis by Dlussky & Pisarski, 1971, and Paraschievescu, 1972; most recently treated as a valid species by Collingwood, 1979, and subsequent authors.]

Formica pratensis var. *ciliata* Ruzsky, 1926. [First available use of the unavailable infrasubspecific name *F. rufa* subsp. *pratensis* var. *ciliata* Ruzsky, 1915]. Synonymy with *nigricans* by Dlussky & Pisarski, 1971. (Note. This name is a junior primary homonym of *F. ciliata* Mayr, 1886).

Formica pratensis var. *cordieri* Bondroit, 1917. *F. cordieri*; Betrem, 1960 (as valid species); Betrem, 1962 (as junior synonym of *nigricans*).

Formica minor subsp. *pratensoides* Gößwald, 1951. *F. minor* **subsp. *pratensoides*; Yarrow**, 1955 (as junior synonym of *nigricans*); Dlusskii, 1967 (as junior synonym of *pratensis*.)

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